

The University of Chicago

ANATOMY OF THE TRANSITION
REGION OF PISUM SATIVUM

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
JOSEPH HARVEY GOURLEY

Private Edition, Distributed by
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Reprinted from
THE BOTANICAL GAZETTE
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ANATOMY OF THE TRANSITION REGION OF *PISUM SATIVUM*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 425

JOSEPH H. GOURLEY

(WITH TWENTY-TWO FIGURES)

Introduction

The general characters of the tribe Viciae of the Leguminosae have been the subject of inquiry by a number of investigators, both from a physiological and from an anatomical standpoint, and although rather well known, many details still remain to be determined. For the present study of *Pisum sativum*, the horticultural variety Champion of England was used. The transition region, investigated in detail, involves the hypocotyl and at least two internodes of the stem.

LESTIBOUDOIS (6) recorded the vascular arrangement in the central cylinder of *Faba equina*, which is similar to that in *Pisum sativum*. He also observed and figured the four cortical bundles, two of them consisting of fibers only and two being fibrovascular in character. The former are on the long axis of the elliptical stem and the latter on the short axis. The vascular bundles of the cortex diverged into the leaves.

VAN TIEGHEM (7) observed the triarch arrangement of the protoxylem bundles of the primary root in *Pisum sativum* with two layers of pericycle between the phloem fibers and the endodermis. He noted that the cotyledons were not opposite, but at an angle of 120° from each other, and that the first leaf occurred on the side of the epicotyl opposite the cotyledons, as it extends upward. Later (8) he studied the cortical bundles in the Viciae, noted the character of the divergence of leaf traces into the petioles, traced the course of bundles in the internodes, and recorded the origin of the two cortical vascular bundles in the cotyledonary region. He followed the course of these bundles through the cortex to the second node, where a branch from each entered the bract. The third node showed the

same plan, except that in addition a small bundle from the stele diverged out through the cortex on each side and became a part of the persistent strands. These somewhat enlarged bundles ended in the true stipules at the fourth node, and new bundles, diverging from the stele, constituted the cortical bundles of the next internode above. There was sometimes a variation from this plan: the prevailing arrangement might occur lower down than the fourth internode or not until the fifth or sixth one.

GÉRARD (3) traced the vascular system of the root and stem of several species, including *Vicia sativa*, which is similar to *Pisum*. He referred particularly to the transition region of these plants, which extended to the fourth internode in *V. sativa*, as also in *Pisum*. He noted the divergence of the leaf trace in toto from the central cylinder into the petiole, and with it the fibrous bundles which occur on the same radius, but located within the cortex. The adjacent lateral bundles of the ellipse were divided in two along a radial plane at a slightly higher level, and were laid down in such a position above the node as to form a leaf trace. Thus the arrangement which repeated the situation at the second node above was reconstructed. HÉRAIL (5) reported the typical arrangement of bundles in the first three internodes of young plants of *Pisum*, although no description was made of the root structure or of the cotyledonary node. He confirmed the work of GÉRARD, but interpreted the fiber strands of the stele as pericyclic rather than phloic.

TOURNEUX (9) pointed out many analogies in the habit of *Vicia*, *Lathyrus*, *Ervum*, and *Pisum*. Much the same anatomical structures were recorded as described by the previous workers. Comment was made upon the protostelic nature of the first internode above the cotyledonary region.

COMPTON (2) observed that seedlings of large species of the Leguminosae exhibit the stable tetrarch arrangement, while a reduction in their size has given rise to an unstable type of tetrarchy. In the Viciae there is a constant triarch arrangement, two xylem strands extending into the cotyledons and the third directly into the plumule. A detailed report was made of the arrangement of bundles at successively higher planes of the first node. The transition region of the first and second internodes was also described, but specific

mention was not made of the relation of exarch and endarch bundles in this region, although the course of the vascular and fibrous bundles was traced.

Methods and procedure

Plants of all ages were removed from the soil in which they were grown, and after being washed free of adhering material, the roots were immersed in a dish or beaker of basic fuchsin stain. The dye was first dissolved in a small amount of alcohol and then diluted with a considerable quantity of water. The vascular system and fibers were stained red by this procedure. The treated plants, or parts of plants, were then boiled for a short time in weak potash (KOH) solution, which softened or dissolved the parenchyma tissue and allowed the fibers and vascular strands to be teased out. The material was placed on a glass plate and kept wet with water or with an aqueous solution of glycerin to prevent rapid drying.

Fresh untreated material, especially cross-sections, were examined by the aid of the binocular dissecting microscope. Certain camera lucida drawings were made from this fresh material that served nearly as useful a purpose as those made from stained and prepared slides.

Material for slides made after the paraffin method was killed and fixed in the following solution: 50 per cent alcohol 100 cc., formalin 7 cc., and commercial acetic acid 2 cc. Safranin and gentian violet were the most useful stains.

Cotyledonary node

The hypocotyl of *Pisum* is short, and no striking difference in arrangement of the vascular bundles of the root is evident until within a few millimeters of the cotyledonary node. Then the vascular group appears suddenly widened, with connecting bands of metaxylem and a wide triangular pith. This is the beginning of the transition from root to stem arrangement, although it continues through the first and second internodes of the stem, and the characteristic stem arrangement is not present before the third internode is reached. CHAUVEAUD (1), VAN TIEGHEM (8), and in fact all writers on this subject have noted this anomalous situation in certain of the

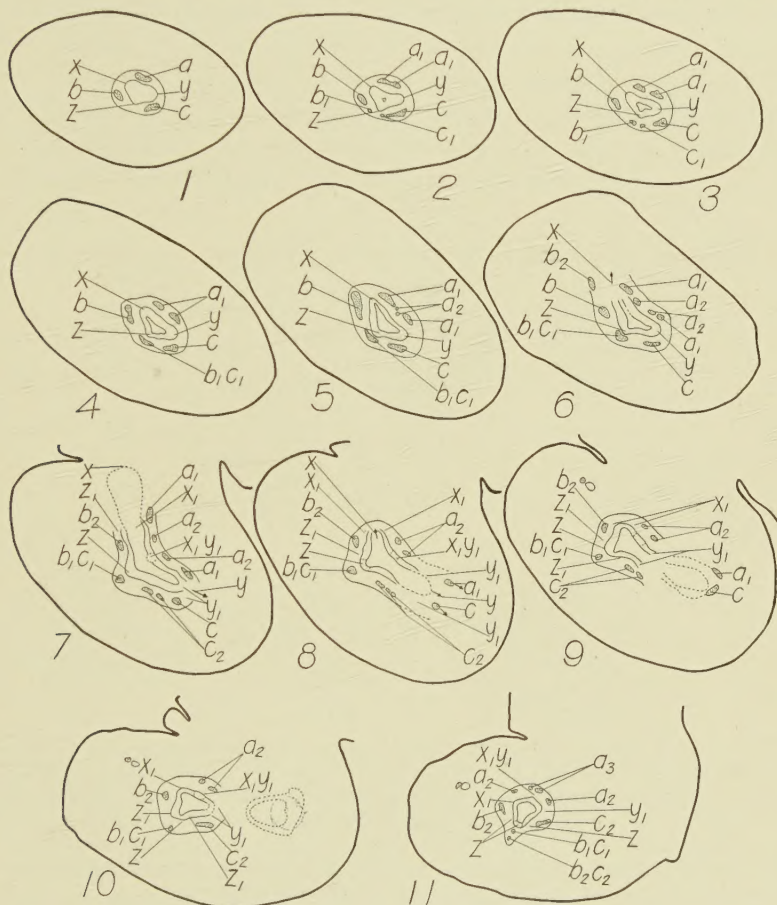
Viciaeae, but it is comparatively rare among other families. Histological details are lacking in most accounts.

1. FIBER BUNDLES

Since the several structures present in a representative cross-section of the root follow somewhat different courses throughout the transition from root to stem, each will be treated separately, beginning with the three bundles of fibers which cap the phloem of the primary root and hypocotyl. The divergence of these fibers can be followed in figs. 1-14, which are sections drawn at successive intervals toward the top of the stem. The approximate location of the endodermis is indicated as the boundary line of the stele. Of the fiber bundles (*a b c*), portions or divergences of each extend into the cotyledons, while diverged portions which are from *b* and *c* are united over the first leaf trace (fig. 5 *z*) and extend into the first internode. Divergences from *a*, *b*, and *c* form the other five fiber bundles present in the cotyledonary node, as follows. Bundle *a* (fig. 1), which is in a plane taken below the node, continues upward and occupies practically the same position in fig. 2, although noticeably attenuated; but at a somewhat higher level it is divided into two portions (fig. 3 *a₁a₁*), which become separated and occupy positions lateral to the xylem mass. Each strand is again divided (fig. 6), small strands (*a₂a₂*) being laid down as extensions from the larger strands, and continuing more or less parallel to them for a short distance, so that in transverse section all four bundles appear in a line and about equidistant from the phloem. Eventually the two strands *a₁* and *a₁* enter the cotyledons (figs. 6, 7), but *a₂* and *a₂* are left as a part of the stelar region. The strands *a₂a₂* continue upward for some distance, becoming more widely separated, and one additional strand diverges from each (fig. 11). These two latter strands (*a₃a₃*) appear as a single strand at a slightly higher level, being then located opposite the phloem of an endarch bundle (fig. 11 leaf trace *x₁y₁*); whereas the strands *a₂a₂* are located at some distance from it, each group closely capping a phloem group of the stele (fig. 12). All the strands continue this arrangement through the first internode of the plant.

In similar manner strand *b* may be followed. Beginning with fig. 1,

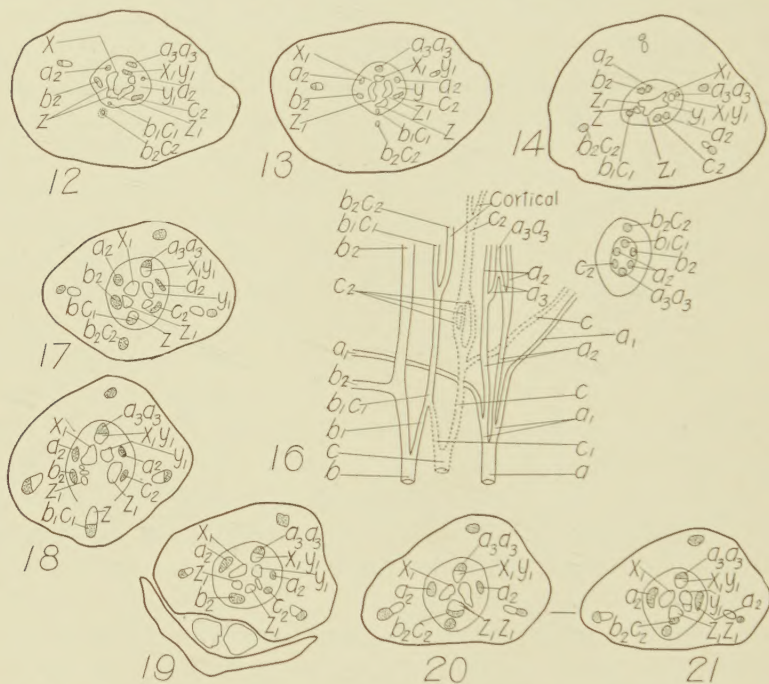
its characteristic position in the root is evident. At a slightly higher level a small portion extends from it at a sharp angle, occupying a position about one-fourth the circumference of the stele from it,



FIGS. 1-11.—Diagrammatic representation of fiber and vascular arrangement of stele and cortex of *Pisum* at successively higher levels through cotyledonary region (see text for explanation of lettering).

approximately midway between bundles *b* and *c*. At about this level, a small strand is extended laterally from strand *c*, and slightly higher still *b*₁ and *c*₁ form a single common strand *b*₁*c*₁, which continues upward for a considerable distance, when *b*₁*c*₁ is divided, the branch

(b_2c_2) occurring on the same radius and exteriorly to it, and eventually being located in the cortex (fig. 13). It is of interest in this connection that in passing through the endodermis into the cortex, this bundle at first has an independent endodermis entirely surrounding it,



FIGS. 12-14, 16-21.—Figs. 12-14, 17-21, diagrammatic representation of fibers and vascular bundles cut at successively higher levels through second node of plant; leaf trace z diverges into leaf at second node, leaving gap in stele in second internode; bundles z_1 and z_2 then united as one endarch bundle at higher level, providing leaf trace z_1z_2 , which supplies leaf at fourth node. Fig. 16, diagram representing perpendicular arrangement of fibers in cotyledonary region: dotted lines represent fiber group which lies on opposite side of stem; lateral divergences supply cotyledons.

while the main stellar endodermis is intact (fig. 15). At a slightly higher level the fiber bundle is surrounded by parenchymatous cells only and the endodermis cells are not differentiated. Bundle b itself is again divided, one of the two divisions passing into the cotyledon along with a vascular strand (fig. 6 x), the remaining portion b_2 continuing as one of the characteristically six fiber groups of the lower stem.

Bundle c , which is the third of the three fiber bundles characteristic of the root, occupies a position analogous to a and b in the lower portion of the hypocotyl. At a slightly higher level a small portion (c_1) on the side toward b is divided from it as already indicated. This smaller bundle (c) passes at an angle toward b_1 , and the two become a single bundle (b_1c_1) which caps a xylem group (fig. 5 z) throughout. Bundle c finally passes into a cotyledon, but previous to doing so three additional small bundles ($c_2c_2c_2$) diverge from it, all three later being merged into a single larger bundle (c_2).

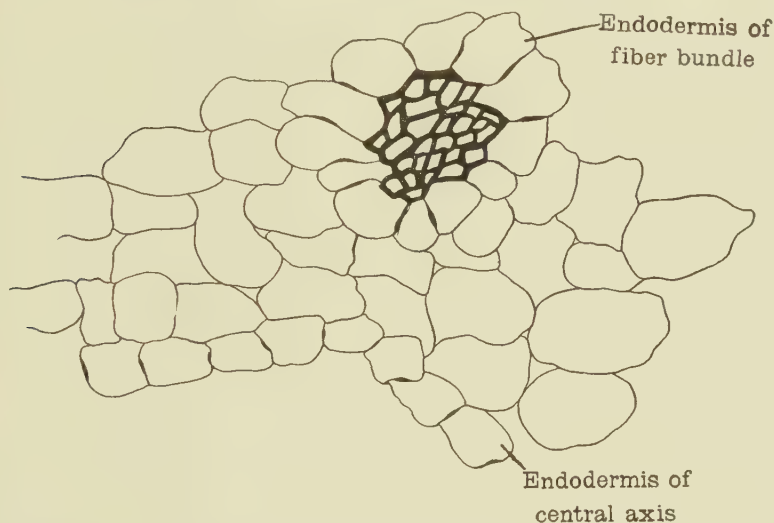


FIG. 15.—Endodermal sheath about fiber bundle which is diverging from stele into cortex; below is shown section of endodermis which surrounds stele; ensheathing endodermis at slightly higher level than that shown in drawing.

Thus at a low level of the first internode, near the cotyledonary node, a transverse section shows fiber bundles a_3a_3 and b_1c_1 capping the phloem of the two leaf traces (x_1y_1z), and two bundles (a_2c_2) (a_2b_2) capping the phloem of each of the two lateral bundles. Occasionally either one or both of the lateral bundles a_2 and c_2 on the one side, or a_2 and b_2 on the other, lie so closely together that they appear as one bundle or nearly so.

Referring again to bundle b_2c_2 , which is located in the cortex at a level indicated in fig. 13, its ultimate disposition may be traced.

When the leaf trace z diverges into a leaf (the details of which are described later), the fiber cap associated with it (b_1c_1) likewise diverges outward and merges with the cortical fibrous bundle (b_2c_2) at the level of leaf departure, and this new bundle subtends the vascular trace in the petiole and leaf ramifications. Above the gap in the stelar ring, which is occasioned by the departure of the leaf trace z , the adjacent fiber bundles b_2 and c_2 give off divergences which are laid down progressively nearer to one another until they finally appear as one, and occupy a position analogous to bundle b_1c_1 below the node just described. A divergence from this new bundle is laid down in an outward direction, and it may be seen in a transverse section of the stem somewhat higher up, occupying a position analogous to that of b_2c_2 in the cortex. Thus a fiber arrangement is reconstructed in the second internode, which provides for a repetition of the divergences at the fourth node.

Similarly, on the opposite side of the stem, the fiber bundle (a_1a_1) associated with leaf trace x_1y_1 gives off a divergence in the lower portion of the first internode which occupies a position in the cortex on the same radius as a_3a_3 . This bundle is not indicated at the level of the stem shown in fig. 13, but is found a few millimeters above that level (fig. 14). These two fiber bundles diverge and subtend the vascular trace of the leaf as one bundle at the third node, in exactly the same way as occurs on the opposite side of the stem at the second node. Then branches diverge from the lateral fiber bundles a_2 and a_2 , which are laid down in such a way as to provide a new fiber bundle to cap the phloem of the leaf trace of the third internode. An outward divergence from this one constitutes the cortical fiber bundle of the third internode. This procedure recurs at each node, alternating from one side to the other throughout the subsequent nodes and internodes of the plant. Fig. 16 shows in diagram the sequence of divergences through the cotyledonary region into the lower portion of the first internode.

2. VASCULAR BUNDLES

The root of *Pisum* is commonly triarch, although there are departures from this arrangement. Since not all the groups of the xylem are associated with like structures at higher levels, the three

points as seen in cross-section are designated x , y , and z respectively (fig. 1), x and y representing the bundles which finally terminate in the cotyledons, and z in the first leaf. In the root there is no pith, but in the hypocotyl, especially near the cotyledons, there is a central pith. There are a larger number of metaxylem elements in the upper hypocotyl, so that a continuous band of metaxylem borders the triangular pith and connects the groups of protoxylem. The triangular outline is much changed (fig. 5), x and y being spread outward near the two cotyledons. At the same time fewer and fewer metaxylem elements are laid down interiorly, but instead parenchyma appears (constituting pith) and metaxylem elements are laid down toward the outside, resulting in mesarch bundles in place of the exarch ones which occur just below. Finally the internal metaxylem of these two diverging groups disappears entirely, and the bundles which actually enter the cotyledons are endarch in arrangement. In this transition from the exarch through mesarch to the endarch situation there is an interspersion of parenchyma cells, so that the conventional type of one or the other is not existent at all levels.

As indicated, there is an increase in the metaxylem elements between the points x , y , and z , which are interspersed with a considerable number of parenchymatous cells, so that the sheath or envelope of the pith does not consist entirely of vessels. Slightly higher up (fig. 5) scattering protoxylem elements appear to the inside of this metaxylem band, which are finally grouped at a point opposite the first leaf trace (z), and additional metaxylem is laid down exteriorly to them. This arrangement results in the endarch bundle which supplies the second leaf or bract (fig. 7).

At the same time that the protoxylem elements are being laid down in a group which forms a part of the second leaf trace, parenchyma appears at either side of the two leaf traces, separating the latter from the more or less continuous band of vessels which envelop the pith at, or slightly above, the level indicated in fig. 7. Protoxylem cells then occur where the metaxylem bands are cut off from the leaf traces. After the traces x and y have diverged into the cotyledons, the ends of the vascular cylinder, bounding the two gaps, and represented at x_1x_1 and y_1y_1 (fig. 9), gradually become continu-

ous by the laying down of additional metaxylem. This makes possible the grouping of x_1x_1 and y_1y_1 into two continuous bundles with protoxylem points at each end, thus constituting the exarch lateral bundles of the stele as shown at the base of the first internode (fig. 13). These changes in arrangement and configuration in the cotyledonary node can be followed at the levels indicated in figs. 1-14.

In detail, the change of the first leaf trace (z) from an exarch group in the root and lower hypocotyl to an endarch one in the first internode is as follows. Toward the upper region of the hypocotyl this vascular group arches out somewhat, parenchyma cells are interspersed with metaxylem, and a little higher the protoxylem elements appear somewhat scattered, owing to the differentiation of parenchyma cells. At a slightly higher level, metaxylem fails to differentiate interiorly to the protoxylem, but elements of it are laid down outside, producing an exarch vascular bundle. Throughout there are some parenchyma cells associated with the vessels of this trace.

At the level indicated in fig. 11 there are more or less definite, although narrow, bands of parenchyma separating the elements of this leaf trace from those of the adjoining groups. This separation is higher in the structure than the separation at points x and y . The points of the lateral bands of metaxylem are therefore designated z_1 and z_1 ; and, as already noted, protoxylem cells are laid down near the point of separation and actually become associated with these points. It is in this way that two of the four exarch bundles of the lower stem are produced.

By the coalescing of the lateral groups y_1 and z_1 on the one side and x_1 and z_1 on the other, continuous lateral strands are formed. At first a rather large pith occupies the central portion of the stem, but at a higher level of the first internode metaxylem cells are laid down until the central portion is completely occupied by them. Before the summit of this first internode is reached, however, parenchyma cells are differentiated within the central portion of the stem, and the siphonostele arrangement is established, which arrangement persists throughout the remainder of the stem. Above the seventh or eighth node the pith disintegrates on maturity and the stem is hollow, except at the nodes where there are constrictions.

Stem

1. EPICOTYLEDONARY INTERNODE

The general arrangement of structures as seen in cross-section of the stem near the base has been noted elsewhere (figs. 3, 4, 7, 8), and is diagrammed in fig. 14. The characteristic arrangement of the primary xylem is much as though two somewhat flattened elongated crescents, with their flattened edges in contact, were placed at the center of the stem, the tips of each crescent being the protoxylem and the space between them being occupied by the metaxylem. Between the divergent tips at each end of the xylem mass, and separated from them by parenchymatous cells, is a small endarch bundle. Thus there appear to be four exarch and two endarch bundles in close association, the stele being neither completely protostelic nor siphonostelic in character.

The two "polar" endarch bundles on the long axis of the elliptical stem are leaf traces. One of them (figs. 1-14 z) supplies the central lobe of the trifid bract at the second node. The other is the vascular supply for the second leaf bract. Near the second node the leaf trace diverges outward through the cortex, enters the bract in toto, and represents the principal central vascular bundle of this leaf. As this divergence takes place, a narrow pith is laid down in the long axis of the elliptical stele, extending from the diverging leaf trace to about its center. The beginning of radial parenchyma rays, which later extend through the lateral xylem groups, originate before the leaf trace has entirely traversed the cortex in its outward course to supply the bract at this second node.

2. SECOND INTERNODE

A section cut immediately above the second node shows only one "polar" bundle, together with the central mass of xylem already referred to and a central pith. Opposite this remaining polar bundle is a leaf gap, which occupies a position homologous to the one which bundle z occupied below the node; the parenchyma of the pith and the gap are therefore continuous.

At a slightly higher level there is a reorientation of the exarch masses of xylem which border the gap together with the accompanying phloem. The central mass of xylem is no longer continuous be-

cause of the laying down of parenchyma cells, rather than metaxylem ones, in the central region, thus dividing the two exarch groups nearest the leaf trace. Parenchymatous cells also separate these adjacent exarch groups from the rest of the xylem mass, as a result of the laying down of such cells rather than metaxylem at that level. These radial divisions are not wide, but serve to separate the central mass into three groups, namely, the two exarch vascular strands bordering the gap and the remainder of the stellar xylem.

The exarch masses adjacent to the leaf gap (fig. 14 z_1z_1) now assume a different position relative to the rest of the central mass, as indicated in sections cut progressively higher up the stem (figs. 17-21). Just as parenchymatous cells were differentiated instead of certain of the vessels in the vascular bundles (z_1x_1 and z_1y_1), so similar cells occur between the tips of these two adjacent exarch masses, so that they form small vascular strands bordering the gap. Then metaxylem is laid down exteriorly, as a part of these groups, with the protoxylem points remaining interior in their relation to the former. The two strands are laid down progressively nearer until they finally appear as a single endarch bundle (fig. 20), which is the trace that supplies the leaf at two nodes above this point (the fourth one of the plant). The general effect is that of the two groups (z_1z_1) adjacent to the gap moving around at an angle of 90° , until they occur as a single vascular bundle which has become endarch rather than exarch, because of the changed relation in which the metaxylem elements are laid down. At the same time the associated fiber bundles are also rearranged, as already described. Thus endarch bundles are the only ones that occur on the side of the stem from which the first leaf trace diverged. Two exarch bundles, however, remain on the opposite side in the second internode.

In the upper region of the second internode, which is characteristically short in all horticultural varieties of *Pisum* examined, there is on the opposite side of the stem a repetition of the disposition of bundles already described for the first internode and second node. The leaf trace (fig. 14 x_1y_1) diverges outward through the cortex near the third node. It supplies the central lobe of the trifid bract of this node, leaving a gap immediately above, as occurred at the node below. At the same time that the leaf trace diverges into

the rudimentary leaf, there is a differentiation of primary tissue leading to the formation of an axillary shoot. This occurs also at the other nodes, and higher up there are primordia for flower branches laid down at an angle of about 35° with the stem.

3. THIRD INTERNODE

After the leaf trace has diverged into the bract at the third node, there is a repetition of the reorientation of the two exarch groups which immediately border the parenchymatous gap. By the process of laying down metaxylem elements to the outside of the protoxylem, and the laying down of parenchyma toward the inside, groups are produced which are endarch in character. These groups are so laid down as gradually to approach one another, finally occurring as a single vascular strand which is the leaf trace that supplies the leaf at the fifth node. With this rearrangement there passes the anomalous situation of both exarch and endarch bundles occurring together in the stem, and throughout the remainder of the plant all the bundles are endarch. The stem now assumes a more nearly four-sided shape, becoming increasingly more so in the internodes above. In two of the four corners of the stem are the fibrovascular bundles which supply the leaves, and in the opposite ones are the prominent bundles which supply the stipules.

4. CORTICAL BUNDLES

The bracts which occur at the second and third nodes of *Pisum* consist of three lobes, the central one being interpreted as an undeveloped blade and the lateral ones as undeveloped stipules. This interpretation is borne out by the vascular arrangement. At the fourth node and at all those above, a true compound blade and two large persistent stipules occur. The leaf traces, as already described, provide the chief vascular supply for the blades, and the fibrovascular bundles of the cortex provide the chief ones for the stipules.

The cortical bundles consist of two fiber groups on the long axis of the ellipse, one opposite each leaf trace, and two fibrovascular ones located at approximately right angles to the fibrous ones. One of the fiber bundles supplies the first bract and the opposite one the second bract, as already noted. The cortical fibrovascular bundles are con-

spicuous features of the stem of *Pisum*. They occur on the sides of the stem at right angles to those from which the leaves depart, and have their origin at the first node, from the edge of the vascular bun-

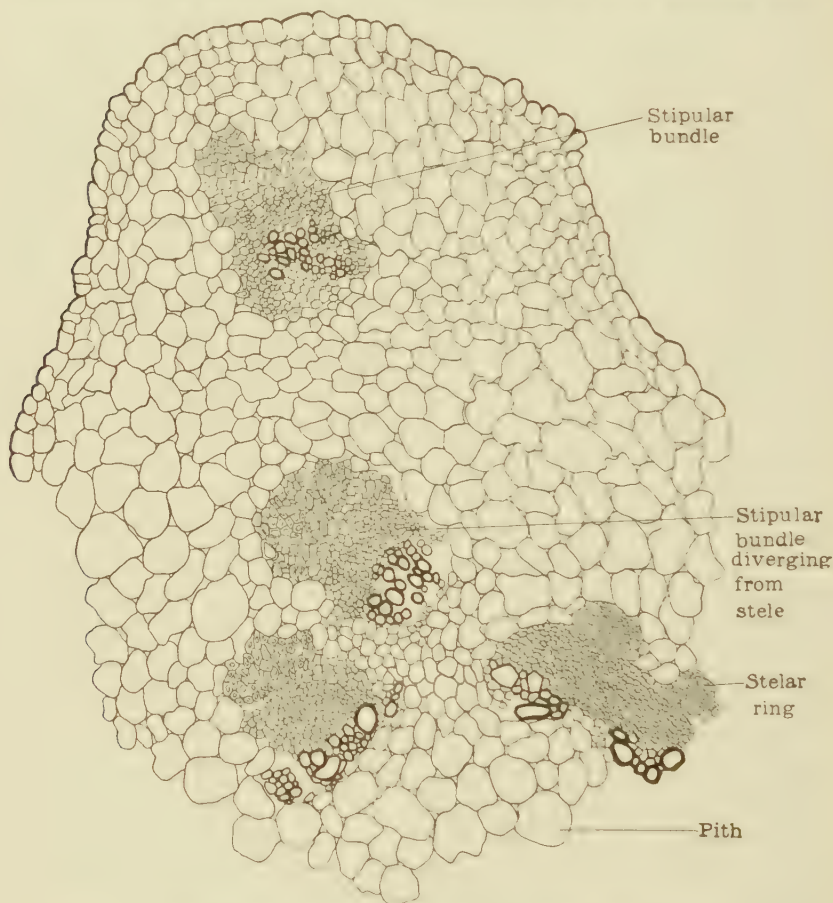


FIG. 22.—Detail of section showing divergence of bundle of stele into cortex; cortical bundle supplies stipule at sixth node.

dles supplying the cotyledons. In some cases two arise on each side, but in such event one of each pair is always small and fades out in the first or second internode. The persistent ones diverge immediately into the cortex, and at the second node a branch from each supplies the outer lobes of the bract, one from one side and one from

the other. Within the bract there is an anastomosis with the leaf trace, so that the bract appears as a single unit. Within the cortex are rather large lacunae at either side of the vascular bundles.

The main portion of the cortical bundles continues up the stem, and at the third node branches diverge to the opposite side and again occur in the outer lobes of the bracts. The main bundles of the cortex continue to the fourth node, where the first true blade and stipules occur. Here the cortical bundles diverge around the stem and enter the stipules in toto at their lowest point of divergence from the base of the petiole, and at approximately right angles to the leaf. They then proceed along the entire line of junction with the stem, ramifying branches extending throughout the stipules. The origin of the vascular bundles which supply the stipules at the fifth node is in the stele. At a short distance below the fourth node, fibrovascular groups diverge out of the stelar ring at opposite sides and at right angles to the leaf traces (fig. 22). These groups are laid down so as to form an outward course into the cortex, and extending upward through the region of the fourth node and the full length of the fourth internode. They then supply the stipules at the fifth node, where they enter them in toto, anastomose in part with the vascular elements of the leaf trace, and together with the latter form the vascular supply of the blade and stipules at this node.

Two gaps in the stele result from the divergence of the fibrovascular bundles, and are evident for a short distance above the departure of the latter. New elements are added to the central cylinder (protoxylem to the inside and metaxylem to the outside), until the gaps no longer exist at a level near the fourth node. This situation is repeated at the succeeding internodes and nodes, providing a pair of cortical bundles for each set of stipules.

Summary

1. The transition from root structure to stem structure in *Pisum sativum* is not complete until the third internode is reached. This anomaly consists in the occurrence of exarch bundles in the first and second internodes, and in a protostelic situation in at least a portion of the first internode.

2. There is a transition in the region of the cotyledonary node

from the triarch arrangement of the root to that of six characteristic vascular bundles in the first internode. These consist of four elongated lateral bundles lying on either side of the small central pith and in the direction of the long axis of the elliptical stem. They appear as two bundles since the metaxylem elements are in contact. All of the bundles are exarch, a smaller bundle lying at either end of the lateral groups, completing the series. Both of the latter are endarch. To the sides of each lateral group are two fiber groups lying about equidistant from the vascular strands, and at either end of the long axis is another fiber group, establishing the complement of six fiber groups within the stelar region.

3. The two smaller vascular groups are the leaf traces that supply the first two alternate leaf bracts. The lateral ones serve in part to supply leaf traces for the fourth and fifth nodes.

4. After the first leaf trace diverges from the stele at the second node, portions of the lateral exarch bundles are laid down progressively nearer together, until they appear as one endarch bundle above the leaf gap. The protoxylem elements occur inward and the metaxylem elements are laid down toward the outside face, producing a new endarch leaf trace. Two exarch bundles remain on the opposite side of the stem in the second internode. At the third node the same rearrangement occurs, so that in the third internode all bundles are endarch and the permanent stem structure is accomplished.

5. There are four cortical bundles in this species, one fibrous one opposite each leaf trace and a fibrovascular group opposite each lateral bundle. The fibrous ones diverge into the blades in toto, and the arrangement is established in the nodes above by divergences from the fiber groups which lie to either side of the leaf gap. The vascular ones are the stipular traces. At the second and third nodes, branches from them supply the rudimentary stipules or bracts and they end free in the first true stipules at the fourth node. Bundles diverge out of the stele in the second internode at right angles to the leaf traces to supply the next node above. This arrangement is repeated at each of the succeeding nodes.

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